NECTAR-SUGAR CONCENTRATIONS AND FLOWER VISITORS IN THE WESTERN GREAT BASIN

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Abstract.— Nectar-sugar concentrations and major flower visitors were determined for 15 species of plants in the Eagle Lake area of Northeastern California. Sugar concentrations for 12 of these are reported for the first time, with means ranging from a low of 10 percent in *Mentzelia laevicaulis* to a high of 63 percent in *Ranunculus uncinatus*. The utilization of the various nectar concentrations varied with the type of flower visitor as well as with the habitat and distributional ranges of the plant and/or animal. Hummingbirds and hawkmoths were not observed visiting the flowers they typically visit in other areas (e.g. *Aquilegia* and *Ipomopsis*, or *Oenothera*), but here preferred more concentrated nectar (*Cirsium* spp., with $\bar{x}$ of 57 percent sugar). Specialization in nectar use is reported at the generic and specific level in Hymenoptera and Lepidoptera; solitary bees, as a whole, used slightly less concentrated nectar ($\bar{x}$ = 38 percent sugar) than butterflies ($\bar{x}$ = 44 percent sugar).

Numerous studies dealing with plant-animal interactions report the importance of flower characteristics such as shape, color, and odor in determining which animals visit a particular species. Recent studies have shown that a correlation also exists between the type of animals which visit a plant and its nectar composition, including the volume of nectar (Heinrich and Raven 1972), types of sugars (Percival 1961, 1965, Wykes 1952), concentration of sugars (Watt, Hoch, and Mills 1974, Baker 1975), and other nectar constituents such as amino acids and proteins (Baker and Baker 1975). In this paper we present data on nectar-sugar concentrations in several nectars utilized by different classes of flower visitors in our study area at the south end of Eagle Lake, Lassen County, northeastern California. The area is characterized by open forests of western juniper (*Juniperus occidentalis*) and Jeffrey pine (*Pinus jeffreyi*), and by more open areas dominated by big sagebrush (*Artemisia tridentata*) and rabbitbrush (*Chrysothamnus nauseosus*). The plant populations used in this study (June to August 1976) were located at elevations between 1530 and 1800 m above sea level; plant names are according to Munz and Keck (1968).

Methods and Materials

Nectar was collected in the field with 10 μl microcapillary pipettes (Drummond Scientific Co.). For extraction from narrow, tubular flowers, the pipettes were drawn out into fine points. Approximately 24 hours prior to nectar extraction the flowers were covered with sheets of porous lens tissue (15 x 20 cm) to keep flower visitors from removing the nectar. The percentage of sugar was determined in the field with a Bellingham and Stanley pocket refractometer, which read up to 50 percent. For nectars more concentrated than this, and for samples smaller than 3–4 μl, an equal amount of distilled water was measured in a second calibrated pipette, and mixed with the nectar sample on the stage of the refractometer. The reading obtained is based on the refractive index of the solution. Nectar sugars in flowering plants consist mainly of sucrose, fructose, and glucose in varying proportions; sucrose is the most widespread and usually predominates (Percival 1961). Sucrose, fructose, and glucose give similar refractive index readings for equal percent solutions by weight (Wykes 1952); therefore, we report our readings as "nectar-sugar," "sucrose," or simply "sugar."

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Flower visitor data were obtained through observations and collection rather than by consulting the literature. On several occasions flower visitors were observed and collected during three time periods (morning, afternoon, and evening), with approximately equal time being spent at each plant species. Flower visitors referred to below as "major" are those which were observed on the flowers on each day (although not necessarily during all three time periods). Representative insect specimens are on file in the Entomology Museum, California State University, Chico.

Results and Discussion

The nectar-sugar concentrations of the 15 species sampled are presented in Table 1. Means of our readings agree fairly closely with those previously reported for three species: *Aquilegia formosa*, 25 percent (vs 32 percent by Baker 1975); *Ipomopsis aggregata*, 25 percent (vs 22 percent by Watt, Hoch, and Mills 1974, and ca 23 percent by Hainsworth 1973); *Oenothera hookeri*, 32 percent (vs 26 percent by Stockhouse 1975). The mean percent sugar contained in the nectars ranged from a low of 10 percent in *Mentzelia laevicaulis* to a high of 63 percent in *Ranunculus uncinatus*. A large variation in nectar-sugar concentrations was also observed within most species. *Asclepias fascicularis*, the most extensively studied species, had nectar-sugar readings ranging from 16 to 72 percent. The openly exposed nectar of this species makes it highly susceptible to environmental factors which cause evaporation and/or dilution; these factors can account, in part, for the wide range of nectar concentrations observed (Stopher, Schlising, and Gut, ms in preparation).

Table 2 is a summary of the major flower visitor types found on flowers of the 15 species of plants studied. Wasp, fly, beetle, and ant visitor types are listed here (and wasps and ants again in Table 3), but since there are no detailed data available for these types they will not be further discussed in

Table 1. Fifteen plant species studied near Eagle Lake, June to August 1976, arranged according to nectar-sugar concentrations. Major flower visitors observed are also listed for each species, roughly in order of importance. Visitor code letters refer to the abbreviations listed in Tables 2–4. Plant names are from Munz and Keck (1968).

Species	Percent Sugar Mean	Percent Sugar Range	No. Flowers Sampled	Flower Visitors
Ranunculus uncinatus	63	62-63	3	Sb Wp Bf Dl Ad Vp Ly Sy Fl Bt At
Cirsium californicum	59	44-74	20	Sb Bb Wp Bf Hm Xy An Os Ag Vp Sp Pp Sy Ml Lm Fl Bt At
Cirsium breweri	54	35-66	28	Sb Bb Hk Hm An Mg Dl Sp
Agastache parvifolia	50	41-76	14	Sb Bf An Os Dl Sy Bt
Asclepias fascicularis	47	16-72	365	Sb Ap Bb Wp Bf Xy An Mg Dl Sh Hy Vp Sp Dn Pp Ly Lm Fl Bt
Scrophularia californica	43	39-49	5	Sb Wp Dl Hy Vp Fl At
Asclepias speciosa	33	21-42	66	Sb Ap Wp Bf Cr An Cl Mg Dl Hy Vp Sp Sn Pp Ly Fl Bt
Oenothera hookeri	32	23-38	25	
Monardella odoratissima	31	17-44	12	Sb Bf Os Sy Ml Bt
Ipomopsis aggregata	25	17-36	33	Fl
Aquilegia formosa	25	14-40	94	Sb Cr
Schoenolirion album	22	16-33	14	Sb Ap Bb Wp Bf Cr Cl Hy Vp Ph Bt At
Pentstemon speciosus	21	14-28	8	Sb Cr Os Dl Hy At
Nocotiana attenuata	21	14-33	27	
Mentzelia laevicaulis	10	7-18	27	Sb Ap Dl Fl
Overall	36	7-76	741	

this paper. All bees other than the honeybee and bumblebees have been grouped under solitary bees. Solitary bees comprise the largest number of flower visiting species in the area and were found on all but three of the plant species studied.

With the exception of *Asclepias fascicularis* (mean nectar concentration of 47 percent sugar), honeybee visits were restricted to the flowers with the more dilute nectars (i.e., concentrations below 35 percent). All of the other flower visitor types preferred more concentrated nectars. However, all of these visitor types had representative species which were found on flowers containing a dilute nectar. *Schoenolirion album*, with an average nectar-sugar concentration of 22 percent, was an especially utilized dilute nectar source. Possible reasons for this were easy accessibility to the nectar, many flowers per raceme, and the fact that this species was one of the very few species locally in flower at the time. Two average sugar concentrations are given for both hawkmoth and hummingbird visitor types due to discrepancies between the flowers they typically visit and the flowers they visited in the study area (see below).

HUMMINGBIRDS.— There was a large difference in the concentration of sugars found in the nectar of the four "hummingbird flowers" but these plants can be grouped into two pairs with similar concentrations (Table 2). One pair consists of two "typical" hummingbird flowers (e.g., Grant and Grant 1968), *Ipomopsis aggregata* and *Aquilegia formosa*, both of which had mean sugar concentrations of 25 percent here, but were not visited by birds. The other two species, *Cirsium californicum* and *C. breweri*, had 59 percent and 54 percent sugar, respectively; these were heavily visited by hummingbirds

TABLE 2. Major flower-visitor types and the nectar-sugar concentrations utilized (of the 15 plant species studied) near Eagle Lake, Lassen County, California.

Visitor Type	No. Species of Flowers Visited	Percent Sugar Mean	Percent Sugar Range
Solitary bee (Sb)	12[a]	38	10-63
Honeybee (Ap)	4	28	10-47
Bumblebee (Bb)	4	46	22-59
Wasp (Wp)	6	45	22-63
Butterfly (Bf)	7	44	22-63
Hawkmoth (Hk)	1	54	
(Hawkmoth	2[b]	27	21-32)
Hummingbird (Hm)	2	57	54-59
(Hummingbird	2[c]	25	25-25)
Fly (Fl)	7	38	10-63
Beetle (Bt)	7	40	22-63
Ant (At)	6	38	25-59
Overall	15	36	10-63

[a]Abbreviations by visitor type names are listed in Table 1 to show which species of flowers were visited.
[b]No visitors were observed, but these plants are expected to be hawkmoth visited (see text).
[c]No visitors were observed, but these plants are expected to be hummingbird visited (see text).

TABLE 3. Major families and genera of Hymenoptera and the nectar-sugar concentrations utilized (of the 15 plant species studied) near Eagle Lake, Lassen County, California.

Visitors	No. Species of Flowers Visited	Percent Sugar Mean	Percent Sugar Range
Anthophoridae	8	39	21-59
Xylocopa (Xy)	2[a]	53	47-59
Ceratina (Cr)	4	25	21-33
Anthophora (An)	5	49	33-59
Apidae	6	38	10-59
Apis (Ap)	4	28	10-47
Bombus (Bb)	4	46	22-59
Megachilidae	8	40	21-59
Osmia (Os)	4	40	21-59
Chelostomoides (Cl)	2	28	22-33
Megachile (Mg)	3	45	33-54
Halictidae	9	42	10-63
Dialictus (Dl)	8	40	10-63
Agapostemon (Ag)	1	59	
Sphecodes (Sh)	1	47	
Colletidae	5	33	21-47
Hylaeus (Hy)	5	33	21-47
Andrenidae	1	63	
Andrena (Ad)	1	63	
Formicidae (At)	6	38	21-59
Vespidae (Vp)	6	44	22-63
Sphecidae (Sp)	4	48	33-59
Overall	12	38	10-63

[a]Abbreviations by bee genus and by nonbee family names are listed in Table 1 to show which species of flowers were visited.

in the study area. Moldenke (1976) does list hummingbirds as especially important pollinators for the genus *Cirsium*. Exact identifications could not be made, but anna's, calliope, and rufous hummingbirds are all known to occur in the area (R. Lederer, personal communication 1977).

Since hummingbirds are high-energy demanding animals, it is advantageous for a cross-pollination-dependent plant to produce a less concentrated nectar and "force" the potential pollinator to visit the maximum number of flowers in order to fulfill its own energy needs (Baker 1975, Heinrich and Raven 1972). Previous studies have found that hummingbirds prefer the less concentrated nectars (Baker 1975, Hainsworth 1973, Hainsworth and Wolf 1972). This is contradictory to our findings, in which hummingbirds did not utilize "their typical flowers" with less concentrated nectars but preferred richer food sources. This has also been found by Stiles (1976), who showed that experimental anna's hummingbirds preferred sucrose and glucose in the highest concentrations available, up to 60 percent. Factors which favor the use of nectar with a weak sugar content may include the disadvantage of a viscous nectar to a bird which must hover while feeding (Weymouth, Lasiewski, and Berger 1964), the difficulty of imbibing and swallowing a more viscous nectar (Hainsworth 1973, Weymouth et al 1964), and the need the birds have for a free water source (Baker 1975). Then what factors, other than nectar concentration, were important in determining hummingbird flower selectivity reported here? Three important factors may be plant population size and density, growth habit of the plants, and the concentrations of the different sugars in the nectar.

Investigations on the energetics of foraging by tropical hummingbirds have shown that large numbers of flower visits are required each day (Wolf, Hainsworth, and Stiles 1972). Gass, Angehr, and Centa (1976) reported that temperate zone hummingbirds defend a territory containing 239 floral units of resource value which is equivalent to that produced by 239 *Aquilegia formosa* flowers. The population of *A. formosa* in the present study contained no more than 100 flowers on any one day. Since no hummingbirds were seen visiting *Aquilegia* here, but were common in the area, it seems density of plants may help determine nectar source. Gass et al (1976) noted that rufous hummingbirds regulate the size of their feeding territories in order to maintain food supplies at a level approximating their metabolic requirements. Also, migratory species feed in a wide variety of habitats each year under a wide range of physiological stresses. Thus, when a territory supplies insufficient energy, the birds' strategy is to seek food elsewhere. This may be the case with hummingbirds we saw, where the populations of *Cirsium breweri* and *C. californicum* were both much larger than that of *Aquilegia formosa* and were in fact the only plants seen visited by the birds.

Gass et al (1976), however, also noted that hummingbirds will feed on the nectar of a preferred species first, even if the population size is too small to meet the birds' energy requirements, and then turn to an alternate source. The fact that we did not observe any foraging on *Aquilegia* may be partially explained by noting that the plants of *Aquilegia* were growing closely interspersed with shrubs, while plants of *C. breweri* especially were located in the open only about 10 m from the *Aquilegia*. The flowers of *Aquilegia* may not have been as readily accessible and energetically favorable for nectar foraging.

The single population of *Ipomopsis aggregata* studied was also small (about 50 flowers at any time), and had the same nectar-sugar concentration as *Aquilegia* and perhaps even a similar floral unit of resource value. This may again suggest that population density could be an important factor in determining the nectar utilization strategy seen in this study.

Yet another possible factor contributing to the nectar selection of the hummingbirds is the proportions of the different sugars in the nectars. The kinds of sugars present were not determined for our Eagle Lake plants; but *Cirsium californicum* sampled

elsewhere was found to have a rather high percent of glucose (58 percent) in the sugars present (I. Baker, personal communication, 1976). Stiles (1976) reported the following hierarchy of sugar preferences in several species of hummingbirds: sucrose over glucose over fructose, with an equal-parts mixture of the three falling somewhere in the middle of the preference order. A nectar containing a large percentage of glucose may be less viscous than one containing a large percentage of sucrose. Thus the high percentage of total sugars in the nectar of *C. californicum* (a potentially highly viscous nectar) may be compensated for by the high percentage of glucose; this may make the nectar less viscous, which, as noted earlier, is advantageous to the feeding of the birds.

HAWKMOTHS.— A situation similar to that with the hummingbirds existed for the hawkmoths and the flowers they visited in our study area (Table 2). No hawkmoths were collected, but common species in the area include *Sphinx perelegans* (Hy. Edw.) and *Hyles lineata* (Fabr.) (from collections at California State University, Chico, and Eagle Lake Field Station). Of the three species of potential hawkmoth flowers present, *Nicotiana attenuata* (Wells 1959) and *Oenothera hookeri* (Baker 1961, Stockhouse 1975) are "typical" hawkmoth-visited flowers (see also Moldenke 1976). They both had rather low average nectar concentrations of 21 percent and 32 percent, respectively. Baker (1975) also found hawkmoth flowers to have lower nectar concentrations similar to those of hummingbird flowers. At Eagle Lake, as with the hummingbird flowers, the hawkmoths were not seen visiting "their typical flowers." Instead, the moths preferred the flowers of *Cirsium breweri*, with a concentrated nectar ($\bar{x}$ = 54 percent). Hawkmoths are homeothermic, hence high energy-demanding ing insects, and in this relatively cool region may require a more concentrated energy source. Also, plant population size was possibly a limiting factor. The two typical hawkmoth plants were represented by very small populations of about 10 individuals each, with 25 open flowers per evening; *Cirsium breweri* heads were very abundant. (Stockhouse [1975] however, found that a single flower of *Oenothera caespitosa* produces an average of 42.1 calories per flower [35 microliters of nectar per night of which approximately 32.5 percent is sugar], which he believes is a large enough potential energy source for hawkmoths even in a small population, with only 20-50 flowers open on a given night. Thus our few flowers of *O. hookeri* could also be a serviceable food source.)

HYMENOPTERANS.— A summary of the major flower-visiting Hymenoptera and the concentrations of nectars they feed on is given in Table 3. Considering the first four families listed (all bees), it is seen that at the family level the mean sugar concentration utilized varied little—from only 38 percent to 42 percent. More specific trends toward nectar selectivity can perhaps be seen within these families. The Anthrophoridae and Megachilidae each had two genera which preferred a more concentrated nectar and a third genus which preferred a more dilute nectar. Although not entirely consistent throughout the data, the genera containing the smaller-bodied species seemed to feed on the less concentrated nectars, and the larger-bodied seemed to utilize the more concentrated nectars. However, at the family level these four means do reflect bee usage, overall, of fairly concentrated nectars. Baker (1975) found the mean percentage of nectar-sugar for 60 species of California native bee flowers to be only 31 percent. In this study bees of a fifth family (Colletidae) preferred nectar with 33 percent sugars, while bees in a sixth family (Andrenidae) fed exclusively on the richer nectar (63 percent sugars) of a single plant species.

The Family Andrenidae in this study was represented by two species, *Andrena* (*Diandrena*) *cuneilabris* Viereck and *A.* (*Euandrena*) *caerulea* Smith (formerly *A. complexa*). These bees restricted their foraging to the flowers of *Ranunculus uncinatus*, which produced the most concentrated nectar (63 percent) found in our samples. In a study done in the Coast Ranges of California, *A. complexa* was found to feed exclu-

sively in the flowers of *Ranunculus californicus* (Linsley and MacSwain 1959). Other species of *Andrena* have also been found to feed almost exclusively on various species of *Ranunculus* (Thorpe 1969, Linsley and MacSwain 1959). Host-specific relationships such as these have usually been described in terms of habitat, flower morphology, and /or pollen source specificity. If nectar concentration and sugar content values are "conservative characters," at least at the genus level (Percival 1961), then the high nectar-sugar concentration in *R. uncinatus* and perhaps other species of *Ranunculus* may also be a factor influencing these host-specific plant-insect interactions.

Butterflies.— Data for the four major families of butterflies found in this study are given in Table 4. The range of means for the nectar is only from 40 percent to 48 percent. In general, butterflies were feeding on a concentrated nectar source. Although data are not given, Baker (1975) reported that nectars of butterfly flowers are slightly less concentrated than those of bee flowers. Our study suggests the reverse: flowers visited by bees had a less concentrated nectar ($\bar{x}$ = 38 percent) than that of flowers visited by butterflies ($\bar{x}$ = 44 percent).

Table 4. Major families and genera of Lepidoptera and the nectar-sugar concentrations utilized (of the 15 plant species studied) near Eagle Lake, Lassen County, California.

Visitors	No. Species of Flowers Visited	Percent Sugar Mean	Percent Sugar Range
Danaidae (Dn)	2[a]	40	33-47
Papilionidae (Pp)	3	46	33-59
Lycaenidae (Ly)	3	48	33-63
Nymphalidae	6	45	22-63
Speyeria (Sy)	4	51	31-63
Melitaea (Ml)	2	45	31-59
Limenitis (Lm)	2	53	47-59
Phycoides (Ph)	1	22	
Overall	7	44	22-63

[a]Abbreviations by visitor names are listed in Table 1 to show which species of flowers were visited.

In their study on plant resources and adult butterflies in a subalpine environment, Sharp, Parks, and Ehrlich (1974) found that butterfly foraging seemed to show opportunistic use of what was available through the season, and no species-specific nectar source relationships were found. Baker and Baker (1975) reported that nectars of butterfly-pollinated flowers are high in amino acids and suggested this may be a factor involved in butterfly foraging strategies, because in most cases this is their only source of these essential chemicals as adults. In this study we did find an apparent specific relationship between a butterfly and its local nectar source. The genus *Phycoides* was represented here by a single species, *P. mylitta mylitta* (Edw.), which restricted its feeding to the flowers of a single species, *Schoenolirion album*. During this study adults were only seen foraging while this plant was in flower, although they are known to visit other flower species (personal observations; Benseler 1975). The nectar produced by this species was much more dilute ($\bar{x}$ = 22 percent) than the nectar of any of the other butterfly-visited flowers. Elsewwhere, *Colias* butterflies have been found to prefer more dilute nectars, probably due to their severe problems of water loss associated with small size (Watt, Hoch, and Mills 1974). Individuals of *Phycoides mylitta mylitta* are also small and may have severe water loss problems in the Eagle Lake area where midday readings of 35 percent relative humidity were of common occurrence. The less concentrated but abundant nectar of *Schoenolirion* may also be an evolutionary trend to early seasonal appearance of both the plant and its visitors. The lack of other flowers "competing" for this potential pollinator may also allow early-flowering *Schoenolirion album* to somewhat limit its nectar-sugar production without lowering chances for cross pollination here.

Conclusions

This study emphasizes several points with data collected in 1976. Data on just 15 species sampled show there was a wide range of nectar-sugar concentrations available to flower visitors found in the Eagle Lake

area. The concentrations produced not only varied from species to species, but they also varied considerably within flowers of the same species. Some of this variation was doubtless caused by local and immediate environmental conditions, but it was still representative of the range of nectar-sugars available to flower visitors there. Various nectar-sugar concentrations were utilized by different types of flower visitors. Data on Hymenoptera and Lepidoptera visitors at the family level show some preferences in the concentrations utilized, but more pronounced preferences were found at the genus or species level of visitor. Species-specific, plant-insect interactions were seen in both of these visitor types in the Eagle Lake area, and the concentration of nectar sugars may be one of several factors influencing these relationships. Factors such as plant population size and density, flower accessibility, and the degree of physiological stress may vary from location to location and affect the utilization of nectar sources by foragers in a given area. This seemed especially true for the hawkmoth and hummingbird flowers, which were not being visited by these animals at Eagle Lake, who preferred more abundant, more concentrated, or more readily accessible nectar.

Acknowledgments

We would like to thank Robbin Thorp for identifying the bees, and Irene Baker and Roger Lederer for supplying unpublished information. We would also like to thank Tim Spira for his critical reading of the manuscript and Mark Stopher for his field assistance. We are grateful for the support of a National Science Foundation Undergraduate Research Participation Grant (SMI 76-03206) that was administered through the Eagle Lake Field Station.

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